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FLOODPLAIN VEGETATION AND SOILS ALONG THE UPPER SANTA ANA RIVER, SAN BERNARDINO COUNTY, CALIFORNIA

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Abstract

The patterns of vegetation and soils were documented in an approximately 20 km^2 area of fluvial terraces adjacent to the Santa Ana River in southwestern San Bernardino County, California. Within this area there are three terraces of differing elevations that were last disturbed during major flood events. The oldest terrace surfaces probably were last disturbed during the Agua Mansa flood of 1862, which disturbed or created many current geomorphic features of the Santa Ana River basin. The most recent disturbance of two other terraces was identified based on photographs of flooding events in 1938 and 1969. Principal component analysis identified three assemblages of species whose distribution corresponded to the three terraces that differed in elevation, soil texture, and age since last disturbance by flooding. Canonical correspondence analysis showed that the assemblages identified by PCA were highly correlated with changes in soil texture and organic matter. The most reliable indicator species were *Heterotheca sessiliflora* and *Lepidospartum squamatum* for the first assemblage (associated with the lowest terrace, and corresponding to early successional assemblages identified by other researchers); *Salvia apiana* and *Senecio flaccidus* for the second assemblage (associated with the intermediate terrace); and *Artemisia californica, Opuntia parryi*, and *Stephanomeria pauciflora* for the third assemblage (associated with the highest terrace). *Eriastrum densifolium* subsp. *sanctorum*, the rare Santa Ana River Woolly Star, was associated with the earlier phases of succession. The most important soil factor distinguishing these assemblages was the silt/clay content of the soil.

Key Words: alluvial scrub, *Eriastrum densifolium* subsp. *sanctorum*, floodplain, Santa Ana River, soil texture, succession.

Much of the floodplain vegetation of the Santa Ana River has been extensively modified by channelization, urban encroachment, or water table lowering, and now may be modified further by the recent construction of the Seven Oaks Dam. This 152.4 m high dam is located where the Santa Ana River emerges out of the San Bernardino Mountains on to a large flood plain that is north of the City of Redlands and south of the City of Highland in San Bernardino County (Fig. 1).

Baxter (1977) and Nilsson and Berggren (2000) have presented extensive discussions of the environmental effects of such dams. A major reported effect is that they dramatically reduce the downstream incidence of flooding and reduce the sedimentation and scouring that are often associated with the rejuvenation of early successional habitats. Dams also trap much of the sediment that would normally be transported downstream, resulting in relatively clear water being released below the dam. Clear water tends to pick up a new sediment load from the area downstream, eroding the stream bed, cutting a deeper stream course channel, and further reducing the likelihood of new sediments escaping the channel and rejuvenating the adjacent habitats in subsequent flooding events.

Vegetation associations in a floodplain often reflect differences in flooding frequency and intensity. Early successional plant species tend to establish in the open areas adjacent to the river course that are more frequently flooded. Species on more elevated sites, which are much less frequently flooded, tend to support mid-successional plant communities. Still more elevated terraces, which are only flooded during extreme events, tend to support late-successional or mature associations characteristic of that geographical region (Blom and Voesenek 1996).

In Southern California, many of the remaining unmodified alluvial valleys, outwash fans, and riverine deposits support an open scrub containing taxa from adjacent coastal sage scrub, chaparral, a few species also found in the California deserts, and several local endemics (Ingles 1929). Hanes (1984) described the vegetation occupying most of the floodplain of the upper Santa Ana River as alluvial scrub. This

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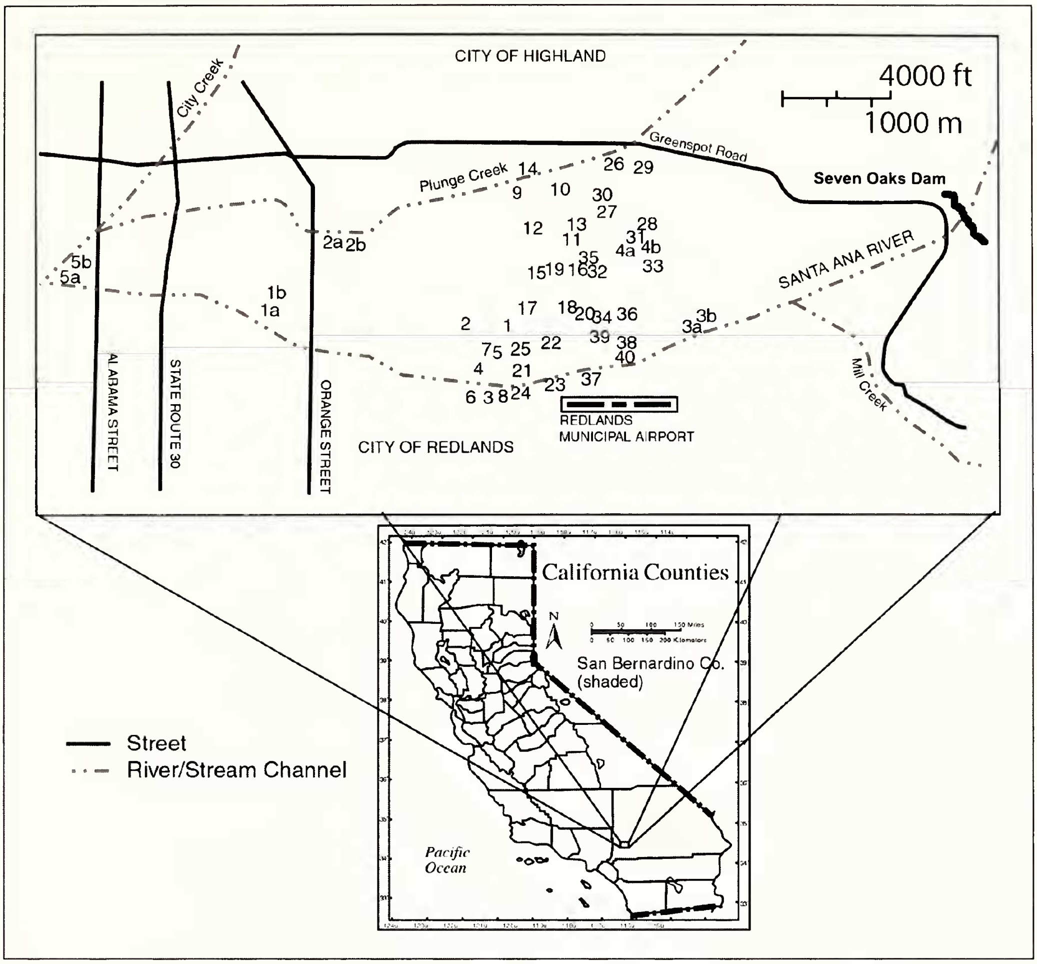

FIG. 1. Locations of the study area and sample sites in floodplain vegetation of the Santa Ana River, San Bernardino County, California. Central map elevation is 425 m. The location of the Seven Oaks Dam is indicated on the far right hand side, just east of where Greenspot Road crosses the Santa Ana River.

vegetation also has been referred to as Riversidean alluvial fan sage scrub (in the California Natural Diversity Data Base/Holland classification [Holland 1986]) and southern alluvial fan scrub (Magney 1992). In *Manual of California Vegetation* (Sawyer and Keeler-Wolf 1995), it is termed the Scalebroom series. In this paper, we refer to this vegetation type as the alluvial scrub community (ASC). It is considered a rare natural community in the State of California, with a Rarefind occurrence ranking of 1.1 (CNDDB 2005).

The alluvial scrub community is distinguished from coastal sage scrub (CSS) by the following qualities: 1) it has a greater variety of evergreen shrubs than CSS; 2) it supports chaparral and desert species (e.g., *Rhamnus crocea* Nutt., Rhamnaceae, *Rhus integrifolia* (Nutt.) Brewer & S. Watson, Anacardiaceae, *R. ovata* S. Watson, Anacardiaceae, *Prunus ilicifolia* (Nutt.) Walp., Rosaceae, *Juniperus californica* Carrière, Cupressaceae, and *Yucca whipplei* Torrey, Liliaceae); 3) *Lepidospartum squamatum* (A. Gray) A. Gray, Asteraceae, (scalebroom) is dominant throughout the ASC and rare in CSS; 4) cover of spring wildflowers is greater than in CSS; and 5) riparian woodland species such as *Platanus racemosa* Nutt., Platanaceae, and *Baccharis salicifolia* (Ruiz Lopez & Pavon) Pers., Asteraceae, occur in alluvial scrub but not CSS.

Early vegetation changes following fluvial surface formation have been described for the ASC of the San Gabriel River floodplain (Smith 1980). Smith identified three seres: an open pioneer stage lasting 30–37 yrs, an intermediate stage, and a mature stage supporting large evergreen shrubs at 40–50 yrs after flooding. She observed that these stages tended to be associated with the frequency of flooding events that scour these surfaces and deposit new sediments.

The recently completed Seven Oaks Flood Control Dam on the main channel of the Santa Ana River will substantially reduce the magnitude and frequency of major flood events and, thus, modify the various riparian communities downstream along the river (Burk et al. 1987), including the ASC. The Santa Ana River ASC is also vulnerable because of sand and gravel mine activity occurring within the floodplain. The construction of the Seven Oaks Dam and the mining activities within the floodplain could reduce the acreage available for early successional species and change the species composition of the ASC.

The upper Santa Ana River supports three endangered species, the Santa Ana River Woolly Star (*Eriastrum densifolium* (Benth.) H. Mason subsp. *sanctorum* (Milliken) H. Mason, Polemoniaceae), the Slender-horned Spineflower (*Dodecahema leptoceras* (A. Gray) Rev. & Hardham, Polygonaceae), and the San Bernardino Kangaroo Rat (*Dipodomys merriami* Mearns subsp. *parvus* (Rhoades) Elliot, Heteromyidae), all of which are associated with this spatially and temporally vulnerable alluvial scrub community. Therefore, it is important to understand the changes in this vegetation type that follow flood disturbance and the timing of these successional changes in order to develop conservation practices to both preserve these species and maintain the diversity of this sensitive community.

The current study reconstructs successional changes following major flood events by characterizing vegetation patterns and edaphic changes after the formation of the surfaces of differing ages (terraces) by erosion and/or deposition within the overall floodplain. Specifically, our objective is to interpret the chronosequence of vegetation and edaphic patterns found on extant terraces that originated following the largest recorded flood, the Agua Mansa flood of 1862.

Specifically, we hypothesized that:

1) the major terraces of differing elevations, soils, and age since last disturbance would have unique species assemblages;
2) species assemblages would be similar in composition to those reported for the San Gabriel River floodplain;
3) increasing canopy cover as reflected in surface light measurements would be a factor in species composition differences found among terraces; and
4) edaphic factors would be related to time since last disturbance of the terrace and would also be related to differences in species composition differences among terraces.

METHODS AND MATERIALS

Study Site. This investigation focuses on an approximately 20 km² area bounded by the City of Redlands on the south, the San Bernardino Mountains on the east, the City of Highlands on the north and the San Bernardino International Airport on the west (Fig. 1). The study site tilts gradually east to west at a 1–2% slope. Geomorphology of the site presents a complex of coalesced alluvial fans originating from the Santa Ana River, Mill Creek, Plunge Creek, and City Creek. The oldest of the geomorphic surfaces are mid– to late–Holocene in age, having been highly modified by overland flow that moves fine sediment, and even gravels and cobbles (Wood and Wells 1996). The alluvial surface is irregularly dissected by channels that have avulsed during major flood events.

Fluvial deposits from these frequently flooded channels are sand and gravel beds that are deposited or reworked during major flood events (Mussetter Engineering, Inc. 1999). The period since the surfaces were significantly reworked by flood events is the time interval for succession. Woodruff (1980) has described the upper Santa Ana River alluvial terrace soils as Soboba stony loamy sand. This Soboba soil series consists of nearly level to moderately sloping soils formed from granitic alluvium on alluvial fans. At our study site, the Soboba series surface is grayish-brown stony loamy sand about 25 cm thick overlying alluvium up to over 100 m in depth. These soils are excessively drained, have low fertility, low water-holding capacity, and very high permeability (Woodruff 1980).

In most years, rainfall events do not result in flows that escape the established river channel and, as a result, do not scour or deposit new alluvium over the existing terraces. Known flood events large enough to shape overbank areas through erosion and deposition occurred in 1862, 1891, 1916, 1927, 1938, and 1969 (Mussetter Engineering, Inc. 1999). The Agua Mansa flood of 1862, with an estimated 320,000 cfs, probably inundated much of the Santa Ana River floodplain, disturbing and modifying all of the terraces within our study area. This flood is characterized as a 100-yr event, that is, one that occurs on average only once in a century (USACE 2000).

The U.S. Army Corps of Engineers (USACE 2000) has simulated these historical flood overflows and concluded that the second largest overflows occurred in the similar magnitude floods of 1891 and 1938 (both with 100,000 cfs). These floods created the somewhat lower terraces that are now considered to be the intermediate-aged terraces. Next in magnitude were the floods of 1916, 1927, and 1969 (two events of 32,460 cfs on 25 Jan. 1969 and a second one of 40,495 cfs on 25 Feb. 1969), which also resulted in overbank flows. Aerial photographs from 1938 and 1969 clearly show that terrace surfaces that we consider to be intermediate- and recent-aged respectively were disturbed by floods in those two years. Flow rates for the 1938 and 1969 floods were recorded on the U.S.G.S. Stream Gauge #11066460 located near Arlington in the City of Riverside, CA (David Lovell, Department of Public Works, San Bernardino County, Personal Communication).

Sample sites. After an analysis of the surfaces (i.e., terrace surfaces) within the study area, sample sites were chosen based on their being included within the three major terraces of differing ages (see Burk et al. 1987 for a detailed map of these terraces). Four sample site locations within the areas created by the 1969 (sample sites 1 and 5) and 1938 (sample sites 2 and 4) floods (Fig. 1) were assigned by two methods. First, ten sites, designated by both numbers (1, 2, 3, and 5) and letters (a–b), were systematically located after mapping the distribution of *Eriastrum densifolium* subsp. *sanctorum* (eds) (Burk et al. 1987). It appeared that several areas that lacked eds were quite similar in vegetation and substrate to adjacent areas containing eds. Therefore, in order to study factors associated with the distribution of this endangered species, sites designated with an "a" were placed randomly within areas occupied by eds, whereas nearby sites of the same age, designated with a "b", contained apparently comparable vegetation but lacked the presence of eds. These plots provided a sampling of terrace surfaces last disturbed during the 1969 and 1938 floods (what we considered to be the young and intermediate–aged terraces).

Forty additional sample sites (grid sample plots) were selected in a stratified random manner on a grid that extended from the northern boundary to the southern boundary through the central section of the floodplain (Fig. 1, all other numbered sites). These sites were selected to thoroughly sample all terraces within the floodplain, including those formed in 1862. The grid contained eight 70 ha cells, each 30 min of latitude and longitude on a side, located from 34°5′00″ to 34°6′30″N and from 117°10′30″ to 117°11′30″W. Six sites were selected per cell: one site in each of the four quarters of the cell and one additional site in both the north and south halves of each cell. Eight sites were subsequently eliminated when they proved to fall outside the floodplain area. Each sample site was located in the field with a Magellan GPS Nav 1000Pro global positioning system (Magellan Navigation, Inc., San Dimas, CA).

Vegetation sampling. In order to characterize the ASC both qualitatively and quantitatively, plant species cover at each site was measured using the line-intercept method (Barbour et al. 1998). In the *Eriastrum* comparison sites, a 100-m base line was randomly placed. Three randomly positioned 30-m line transects were then placed perpendicular to this base line. In the grid-selected sample set, each of the 40 samples consisted of a randomly oriented 50-m line transect placed at the randomly selected grid point. Orientation was constrained in order to keep the entire transect on a single fluvial surface and to avoid structures and disturbances. Intercept length to the nearest 5 cm was recorded for woody plants (by species), plus herbaceous plants, bryophytes/cryptogamic crust, litter, and dead shrubs. No attempt was made to distinguish individual herbaceous species since the majority of the sampling was carried out during the dry season. Almost all of the herbaceous cover consisted of introduced annual grasses and herbs. Nomenclature follows Hickman (1993) and voucher specimens are filed at the Fay A. MacFadden Herbarium (MACF) at California State University, Fullerton.

Soils. Over the long term, as fluvial terraces age their soil properties slowly tend to differentiate (Jenny 1941). However, recent work on similar fluvial terraces in the Cajon Wash (a system that empties into the Santa Ana River just west and slightly south of our study area), has showed that silt and organic matter rapidly accumulates during the first 40 yrs after flooding even in the soils of these terraces (McFadden and Weldon II 1987). Specifically, they argue that the vast majority of this rapid accumulation is due to the influx of eolian (airborne) dust. This influx not only increases the organics but also increases the water holding capacity of these soils. Such changes could affect the rate of plant succession in such soils and have a significant effect on the persistence of particular early successional species.

Therefore, soil samples were collected to determine the extent of silt and organic matter accumulation at our sample sites, using separate protocols for the eds comparison sites and the grid sample plots. For the eds comparison plots, a soil sample was obtained from a random location along each 30-m line transect used for vegetation sampling for a total of three sub-samples from each comparison site. For the grid sample plots, soil samples were obtained by taking five sub-samples at 10-m intervals along the 50-m transect starting from a randomly selected point. Soil samples were obtained in an identical manner at all sites: A 25-cm metal cylinder (10-cm in diameter) was forced vertically into the soil, then the upper 10-cm of soil was removed from the cylinder, and the remaining soil, from 15–25 cm depth, constituted the sample. All samples from each sample site were thoroughly mixed and a sub-sample was removed for analysis.

Soil samples were analyzed for texture, organic matter, and salinity. Samples were sieved through

1.25- and 2-mm screens to separate larger fractions. Approximately 100 grams of the < 2 mm fraction were analyzed for texture using the Bouyoucos hydrometer method (ASTM Method D433) after removal of organic matter by combustion as outlined by Cox (1985). Organic matter content of the < 2 mm fraction was determined gravimetrically after burning a 100 g oven-dried sample in a muffle furnace at 500°C for 24 hrs. Silt, combined with clay, is reported as "fines" and represents the < 0.05 mm fraction. Values reported as sand are for the 0.05–2 mm fraction and gravel is defined as the 2–13 mm fraction.

Salinity was determined using the conductance of the supernatant from a mixture of 20 g of < 2 mm soil and 100 cc of deionized water equated to standard solutions of NaCl mg/l converted to soil osmotic potential using Van Hoff's law (after Burk et al. 1987). The units used in the analysis are conductance units of millimohs per meter.

Light measurements. Light levels were measured at each sampling site using a LiCor Model 170 light meter fitted with a quantum sensor and served two separate purposes. Ambient light 30 cm above the ground was expressed as percentage of full unobstructed light above the plant canopy and provided a measure of light transmission through that canopy. Reflected light from the soil surface, measured by turning the sensor toward that surface, was also expressed as a percentage of full unobstructed light. It was used as an indirect measure of soil coverage and color. All light measurements were taken on days with less than 25% cloud cover and never when a cloud shaded the site. These measures were also taken between 1000 and 1600 hrs Pacific Standard Time only, in order to avoid low sun angles. The maximum unobstructed light value for each point was taken as the maximum for that point in order to standardize the data for sun angle. In all measurements, care was taken to orient the sensor perpendicular to the soil surface. The readings were recorded at 5 m intervals (n = 10) along the transect from a randomly selected starting point with the sensor 30 cm above the ground at each point. The percentage of full light for ambient and reflected light at each subsample was then calculated. The means of the ten measured light percentages were used to obtain the values for ambient and reflected light levels for each sample site.

Ordination. In order to describe the nature of the relationships between the vegetation and the environmental factors, principal component analysis (PCA) and canonical correspondence analysis (CCA) were performed on all 50 sample sites using protocols in CANOCO for Windows (ter Braak and Smilauer 1998). Thirty-six units were analyzed: 33 woody plants identified to species plus the 3 general plant groups (herbaceous, cryptogams, and dead shrubs). However, woody species occurring in only one sample were subsequently omitted from the analysis leaving 23 active "species" under consideration. Sample sites 6, 15, 31, 32, 33, 42, 46, and 48 were also eliminated from analysis since they proved to contain extreme values in either soil or cover, leaving 42 active samples. In both PCA and CCA, centering was focused on species. In CCA, rare species were downweighted and there was no rescaling or detrending. Of the 11 measured environmental variables, four factors (fines, organics, sand, and gravel) made significant contributions to the analysis based on evaluation of inflation factors (Burk et al. 1987; Ryan 1995). Monte Carlo tests of the first canonical axis and all canonical axes were run with unrestricted permutations. CCA ordination plots are biplots of species and environmental factors. No transformations of variables were employed in the analyses.

RESULTS

Descriptive Statistics – Descriptive statistics for species cover data and for environmental variables are presented in Tables 1 and 2, respectively. Eight non-perennial plant categories (i.e., herbaceous ground cover and substrate categories) were encountered on the transects. Of these, grass, bare ground, and dead shrubs had the highest overall mean cover values (Table 1). Thirty species of perennial vascular plants occurred on the transects, many of which were only encountered occasionally. Only five species had mean cover values above 2%: *Eriogonum fasciculatum* Benth., Polygonaceae, *Juniperus californica, Eriodictyon trichocalyx, Lepidospartum squamatum*, and *Adenostoma fasciculatum* Hook. & Arn., Rosaceae. Percent cover as reflected in light measurements did not vary significantly with terrace age. Ambient light (% of maximum) reflected from the soil surface was quite high overall, indicating an open habitat (Table 2).

Ordination. The CCA eigenvalue for Axis 1 (0.152) is three times greater than the eigenvalues for the other axes (Table 3). The eigenvalues of the PCA are 0.71, 0.068, 0.053, and 0.043 for Axes 1–4 respectively. We present both the PCA and the CCA results because PCA eigenvalues are substantially higher for Axis 1, suggesting that the relationship between environment factors and species can be determined with CCA.

Axes 1 and 2 of the PCA suggested three species groups and four species without definitive association (Fig. 2). *Eriogonum fasciculatum* (erf) and *Opuntia litoralis* (Engelm.) Cockerell, Cactaceae (ol) were at opposite poles of both axes from

TABLE 1. DESCRIPTIVE STATISTICS FOR SPECIES COVER DATA. Species are listed in descending order of mean % cover as recorded from forty-two 50 m transects. Most species were not encountered in all transects, therefore zero values were included in the calculation of the means. All forty-two sample sites are included.

Species	Mean ± Standard Deviation	Minimum–Maximum
Grass	32.0 ± 20.5	0.5–64.3
Bare ground	14.2 ± 13.6	0.3–59.5
Dead shrubs	9.5 ± 6.5	0.2–28.9
Eriogonum fasciculatum	6.2 ± 6.8	0.0–32.5
Bryophytes/cryptogamic crust	5.3 ± 5.5	0.0–27.0
Tall herbs	5.1 ± 3.9	0.0–15.4
Stone	3.3 ± 4.4	0.0–25.2
Juniperus californica	3.0 ± 6.6	0.0–22.7
Eriodictyon trichocalyx	3.0 ± 3.9	0.0–15.9
Lepidospartum squamatum	2.5 ± 4.9	0.0–25.2
Adenostoma fasciculatum	2.2 ± 5.5	0.0–24.7
Gutierrezia californica	1.8 ± 0.5	0.0–11.9
Yucca whipplei	1.7 ± 2.6	0.0–13.3
Low herbs	1.6 ± 1.8	0.0–7.0
Lotus scoparius	1.4 ± 1.9	0.0–7.0
Bebbia juncea	1.1 ± 2.9	0.0–11.8
Prunus ilicifolia	0.8 ± 4.3	0.0–26.4
Opuntia littoralis	0.8 ± 1.3	0.0–4.8
Salvia apiana	0.7 ± 2.3	0.0–11.0
Encelia farinosa	0.6 ± 1.9	0.0–8.0
Artemisia californica	0.5 ± 1.5	0.0–7.1
Mirabilis californica	0.5 ± 1.2	0.0–5.5
Rhus ovata	0.4 ± 1.9	0.0–12.3
Stephanomeria pauciflora var. *pauciflora*	0.3 ± 0.8	0.0–4.3
Ericameria pinifolia	0.3 ± 0.9	0.0–4.4
Opuntia parryi	0.3 ± 0.7	0.0–2.8
Bunchgrass	0.2 ± 0.8	0.0–3.8
Eriastrum densifolium subsp. *sanctorum*	0.2 ± 0.8	0.0–5.1
Phoradendron densum	0.1 ± 0.5	0.0–3.1
Cercocarpus betuloides	0.1 ± 0.7	0.0–4.3
Marah macrocarpus var. *macrocarpus*	0.1 ± 0.5	0.0–3.0
Solanum xanti	0.1 ± 0.4	0.0–2.2
Senecio flaccidus var. *douglasii*	0.1 ± 0.3	0.0–1.8
Cuscuta sp.	0.0 ± 0.3	0.0–1.8
Gnaphalium californicum	0.0 ± 0.2	0.0–1.5
Croton californicus	0.0 ± 0.1	0.0–0.7
Dudleya lanceolata	0.0 ± 0.0	0.0–0.1
Calystegia macrostegia	0.0 ± 0.1	0.0–0.4

TABLE 2. DESCRIPTIVE STATISTICS FOR MEASURED ENVIRONMENTAL VARIABLES. All forty-two sample sites are included.

Variable	Mean ± Standard Deviation	Minimum–Maximum
Litter cover (%)	56.9 ± 26.8	0.0–99.0
Clay particulates (%)	2.4 ± 1.0	0.2–4.3
Silt particulates (%)	7.0 ± 3.5	1.7–15.6
Sand particulates (%) – (sand)	90.5 ± 3.5	82.3–96.2
Fine particulates (clay + silt %) (fines)	9.5 ± 4.1	3.9–17.7
Salinity/conductance (millimohs/m)	0.4 ± 0.3	0.1–1.0
Organic Matter (% dry weight) – (Organics)	0.6 ± 0.6	0.2–4.0
2–13 mm soil particles (% dry weight) (gravel)	10.5 ± 6.9	2.1–33.6
< 2 mm soil particles (% dry weight)	87.7 ± 7.7	65.3–97.6
Ambient light (% of maximum)	81.3 ± 11.2	50.6–99.6
Reflected light (% of maximum)	8.2 ± 3.3	4.2–23.6

TABLE 3. SUMMARY OF CANONICAL CORRESPONDENCE ANALYSIS OF FLOODPLAIN COMMUNITIES OF THE SANTA ANA RIVER NEAR REDLANDS, CALIFORNIA. Input data included 42 samples, 23 species with 490 occurrences and 4 environmental variables. ** Indicates that a particular canonical axis was significantly ($P \leq 0.01$) correlated with environmental factors.

Statistic	Axis 1	Axis 2	Axis 3
Eigenvalue	0.152	0.057	0.035
Species/environment correlations	0.677**	0.5989**	0.579**
Cumulative % variance of species data	9.6	13.2	15.4
Cumulative % variance of species-environment relation	58.1	79.8	93.2

Juniperus californica (jc) and *Lotus scoparius* (Nutt.) Ottley, Fabaceae (los) and thus had quite different affinities and are not included in any of the three groups. (Species are identified with symbols used throughout this paper.)

The CCA correlations between species and environment ranged from 0.462 for Axis 4 to 0.677 for Axis 1. The relationship between species and the four environmental variables was highly significant ($P \leq 0.01$). The cumulative percent of the variance of the species-environment relation indicates that the environmental conditions measured were probably important contributors to species distribution.

The CCA biplots of species scores and environmental factor scores in Fig. 3A showed that Axis 1 was related first ($r = -0.61$) to the amount of fines and secondly to organics ($r = -0.47$). Axis 2 was related ($r = -0.32$) principally to organics. Axis 3 was related to gravel ($r = +0.49$) and sand ($r = -0.51$) (Fig. 3B). Table 4 presents the statistics on the major environmental variables. The relationship between individual species and the environmental axes as determined from t-value biplots showed that multiple species had significant correlations with the environmental axes (Table 5).

When species scores in Fig. 3A were projected to the lines representing fines, three groupings of species were apparent. *Heterotheca sessiliflora* (Nutt.) Shinn., Asteraceae (hf), *Encelia farinosa* Torrey & A. Gray, Asteraceae (ef), and *Lepidospartum squamatum* (ls) were consistent indicators of soils with the least silt and clay content. All of the species that fell on the negative side of Axis 1 were associated with higher silt/clay content and formed a second group that, with the exception of the outlier *Croton californicus* Muell. (Euphorbiaceae [cc]) were the members of PCA Group 3. The third cluster had affinity with soils of intermediate silt/clay content and included all species between *Yucca whipplei* (yw) and *Ericameria pinifolia* (A. Gray) H. M. Hall (Asteraceae [ep]). The third cluster was a mixture of PCA Group 2 and 3 species. Organics correlated with Axes 1 and 2 almost equally and were the only important correlate of Axis 2. Therefore, little interpretable separation occurred on Axis 2. CCA Axis 3 was correlated almost equally with sand and gravel (Fig. 3B). When species centroids were projected perpendicular to the line representing sand, the species from PCA Group 1 formed a group at higher concentrations of sand. PCA group 2 intermingled with PCA Group 1 on Axis 3.

The last two columns in Table 5 show the axis tolerance for each species on Axes 1 and 3 of the CCA ordination. A low value indicates a narrow niche breadth for the principal environmental factor driving each axis and thus identifies indicator species for each PCA group. Axis 2 is not included because of a lack of interpretable separation on that axis.

DISCUSSION

Species cover data document that the upper Santa Ana River alluvial zone is an open habitat supporting a diversity of annual and perennial plant species including, in some, but not all sites, the rare Santa Ana River Woolly Star (eds). Measured environmental variables show that the soils are characterized by a high content of sand or particles > 2 mm in size and that the percent of ambient light reaching the soil surface is quite high in all terraces, again indicating that the habitat is quite open. These features are expected in periodically flood-rejuvenated floodplain habitats.

Regarding succession within alluvial scrub, our findings are consistent with those of Smith (1980) and Hanes et al. (1989) who concluded that there are three seral stages apparent in southern California alluvial scrub vegetation following major disturbance of terraces by flood. Our data, however, suggest much longer periods of dominance for each seral stage and redefine the two later seral stages described by Hanes et al. (1989) and Smith (1980).

In our data, terraces differed in plant assemblages, soil attributes, and time since a major flood disturbance. The dominant plants and edaphic conditions that characterized each of the terraces are as follows. The first asemblage was indicated by the presence of *Lepidospartum squamatum* and/or *Heterotheca sessiliflora.* Terraces that were modified by the 1969 flood supported this assemblage. *Encelia farinosa* was also dependably found on soils characterized by high sand, and low organic and clay content

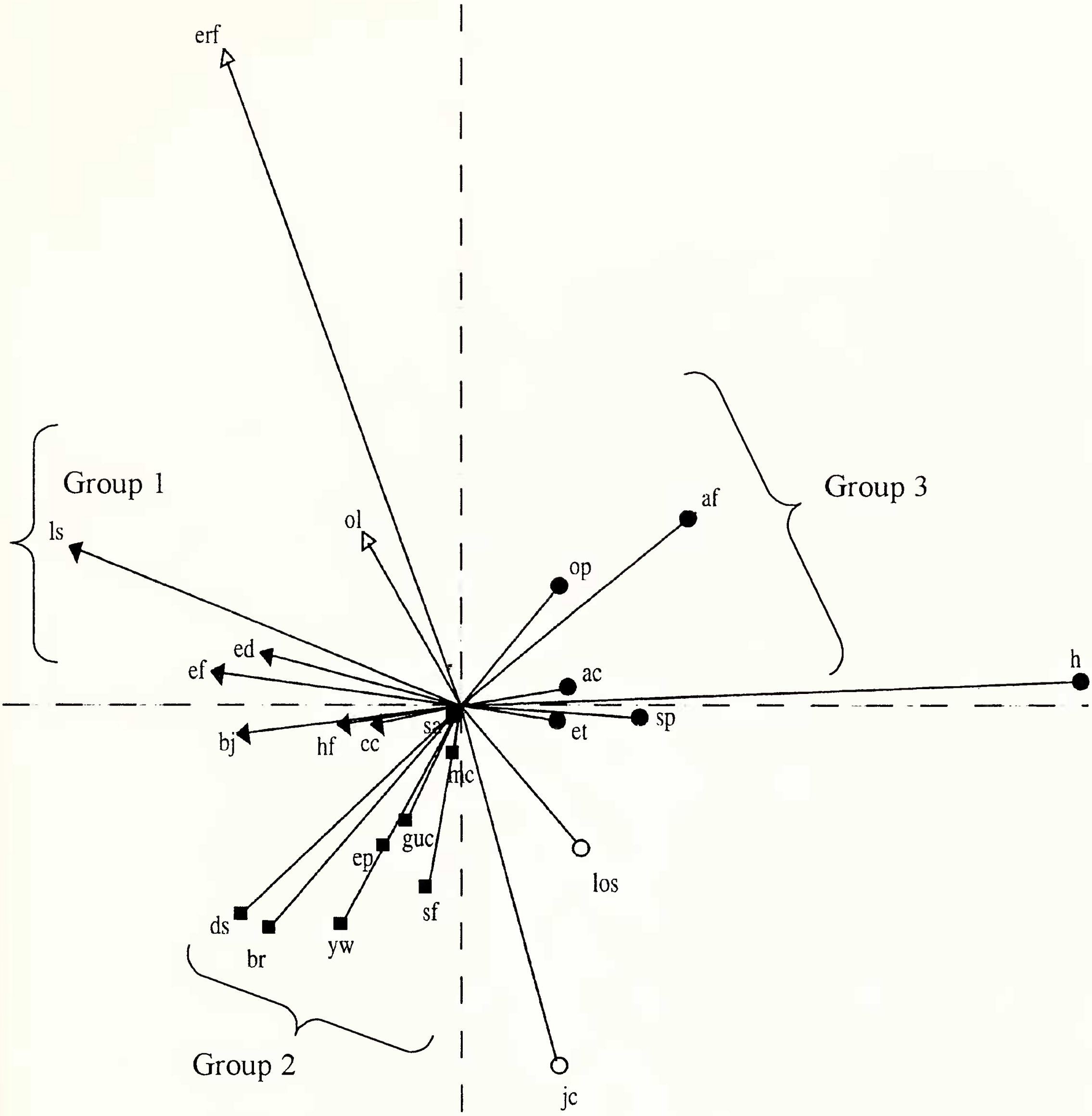

FIG. 2. Principal components analysis axis 1 (horizontal) and axis 2 (vertical) for upper Santa Ana River floodplain species scores. The delimited groups are the PCA groups referred to in the text. Open symbols represent species with no group affinity. Species codes are explained in Table 5. In comparison to Fig. 3, this figure is rotated 180°.

(which were characteristic of the lower elevation terraces disturbed by the 1969 flood), but was not widely distributed. Other plants with centroids in the first assemblage included the endangered *Eriastrum densifolium* subsp. *sanctorum* and the more common *Bebbia juncea* (Benth.) E. Greene (Asteraceae). *Croton californicus* also had its centroid in this group but it was generally distributed and, therefore, was of little value as an indicator.

Hanes et al. (1989) and Smith (1980) refer to this first assemblage as the pioneer community. It is pioneer only in the sense of being first after flood. It contains essentially no ruderal (r-selected) species, probably because the washed sand substrate lacks nutrient and water holding capacity and is, therefore, nutrient limited. *Eriogonum fasciculatum* was not clearly associated with this early seral stage in our data; rather it proved to be an isolated species whose distribution was difficult to interpret. However, Smith (1980) and Hanes et al. (1989) did find that *E. fasciculatum* was an early successional species, unlike the case in our study.

The character of the other two assemblages in our study differed significantly from the intermediate and mature stages described by Hanes et al. (1989) and Smith (1980). *Malosma laurina*

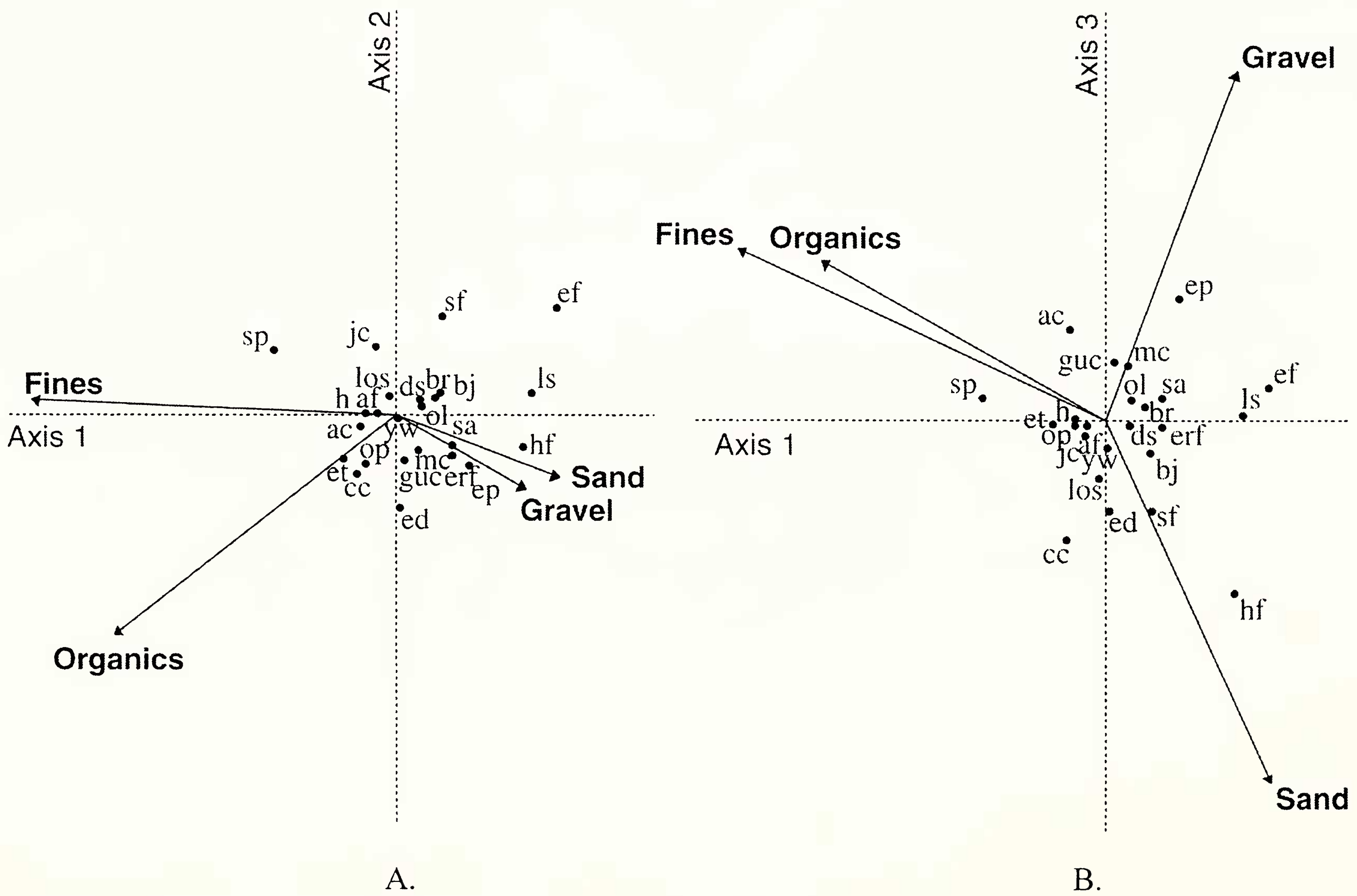

FIG. 3. Ordination diagrams from canonical correspondence analysis showing the distribution of plant species on (A) axes 1 and 2 and (B) axes 1 and 3 relative to 4 environmental gradients in floodplain communities of the upper Santa Ana River, California. Species codes are listed in Table 5.

TABLE 4. SUMMARY STATISTICS FOR SOIL FEATURES INCLUDED IN THE CANONICAL CORRESPONDENCE ANALYSIS OF FLOODPLAIN VEGETATION ALONG THE UPPER SANTA ANA RIVER, CALIFORNIA.

Statistic	Gravel	Sand	Fines	Organics
Mean (%)	9.2	82.0	8.5	0.4
Standard deviation	6.0	10.1	4.7	0.2
Minimum	0.7	61.3	1.4	0.1
Maximum	23.2	98.6	17.7	1.0

(Nutt.) Abrams (Anacardiaceae), *Rhus integrifolia, Ribes aureum* Pursh. (Grossulariaceae), and *Salvia mellifera* E. Greene (Lamiaceae), which Smith (1980) considered indicators of the mature stage, did not occur in our samples and are uncommon in the upper Santa Ana River floodplain. Smith indicated that her mature stands were 47+ years old, which roughly corresponds to the age of stands on terraces last disturbed in 1969 in the current study.

The second assemblage on the upper Santa Ana River alluvial zone supports *Senecio flaccidus* Less. (Asteraceae) and *Salvia apiana* Jepson (Lamiaceae), which had narrow distributions on soil gradients, and were, therefore, good indicator species. Additional shrubs with centroids in the intermediate assemblage were *Ericameria pinifolia* and *Yuccca whipplei.* The presence of cryptogamic crust and dead shrubs was also noted in this phase. Other species found in the second assem-

TABLE 5. LIST OF SPECIES INCLUDED IN THE SAMPLES. Codes and PCA Group are included for those species in the ordinations. A (?) indicates an unclear group affiliation, an (*) indicates a significant ($P \leq 0.05$) correlation between the species and the environmental factor and (ns) indicates non-significance. Axis tolerance is the root mean squared deviation for each species on axes 1 and 3.

Species	Code	PCA Group	Fines	Organics	Sand	Gravel	Axis 1 Tolerance	Axis 3 Tolerance
Adenostoma fasciculatum	af	3	ns	ns	*	ns	0.97	0.92
Artemisia californica	ac	3	ns	ns	*	*	0.76	0.90
Bebbia juncea	bj	1	ns	ns	*	*	0.76	0.86
Croton californicus	cc	1	ns	ns	ns	ns	1.63	0.78
Encelia farinosa	ef	1	*	*	*	*	0.24	0.43
Eriastrum densifolium	ed	1	*	ns	*	*	1.68	0.85
Ericameria pinifolia	ep	2	*	*	*	*	1.24	1.20
Eriodictyon trichocalyx	et	3	*	*	*	*	1.18	0.88
Heterotheca sessiliflora	hf	1	*	ns	*	*	0.04	0.29
Juniperus californica	jc	?	*	ns	*	*	0.81	0.79
Lepidospartum squamatum	ls	1	*	*	*	*	0.86	1.29
Lotus scoparius	los	?	*	ns	ns	ns	0.76	0.60
Mirabilis californica	mc	2	*	ns	*	ns	0.80	0.93
Opuntia litoralis	ol	?	ns	*	*	*	0.88	1.07
Opuntia parryi	op	3	*	ns	*	*	0.74	0.92
Salvia apiana	sa	2	*	*	*	*	0.39	0.66
Senecio flaccidus	sf	2	*	ns	*	*	0.31	0.18
Stephanomeria pauciflora	sp	3	*	*	*	*	0.54	0.97
Yucca whipplei	yw	2	ns	ns	ns	ns	0.88	1.11
Herbaceous plants	h	3	*	*	*	*	0.89	0.98
Dead shrubs	ds	2	*	*	*	*	0.99	0.97
Cryptogams	br	2	*	*	*	*	0.80	1.04

blage were *Gutierrezia californica* (DC.) Torrey & A. Gray (Asteraceae), and *Marah macrocarpus* (E. Greene) E. Greene (Cucurbitaceae). This assemblage was associated with terraces last disturbed by the 1938 flood.

Species with narrow tolerance for soil characteristics in the third assemblage were *Artemisia californica* Less. (ac, Asteraceae), *Opuntia parryi* (op) and *Stephanomeria pauciflora* (Torr.) Nutt. (sp, Asteraceae). Also included in the mature stage were *Eriodictyon trichocalyx* A. A. Heller (Hydrophyllaceae), and *Adenostoma fasciculatum. Lotus scoparius* and *Juniperus californica* appeared to be members of both the second and third assemblages.

These second and third assemblages did not correspond to those of Hanes et al. (1989). Hanes (1989) did not differentiate the juniper woodland and chamise associations in terms of environmental variables or stand age, which may be why he assumed that the juniper woodland was associated with a late successional sere. In contrast, in our data, *Adenostoma fasciculatum* was a member of the second assemblage, and *Juniperus californica* was a member of the second and the third assemblages.

Annual herbaceous plants, primarily introduced grasses, were not widespread in this vegetation except on higher terraces. The greater concentrations of clay, silt, and organics on these terraces indicate that sufficient resources exist to support both these resource-demanding grasses and the shrub species of the second and third assemblages that dominate the vegetation of these terraces.

The character of alluvial scrub vegetation of the upper Santa Ana River is highly correlated with soil features that are associated with terrace elevation and likely change gradually with time since the last major flood. In contrast to Smith (1980), we found that changes in alluvial scrub vegetation were correlated with quite small changes in soil texture. In general, with time since last disturbance, there is a gradual increase in the silt/clay and the organic fractions and a coinciding decrease in the relative amount of sand in the soil. These findings are in agreement with those found by Dorronsoro and Alonso (2006) for the fluvial terraces of the Almar River near Salamanca in central western Spain.

The extent to which soil attributes change with time since disturbance is difficult to ascertain. The largest floods on record occurred during the 1860's, including the Agua Mansa flood of 1862. It is generally accepted that the current geomorphology of the upper Santa Ana River was established at that time (Mussetter Engineering, Inc. 1999). Individual *Juniperus californica* trees at one of our sites (2a and b) were established in the late 19th century (personal observation of growth rings indicated they were approximately 100 yrs old). This site fell into our third assemblage, which was associated with the higher elevation terraces, greater clay and silt contents, and the longest interval since disturbance by flooding; this site supported early phase indicators only in isolated microhabitats where rodents or small stream channels have exposed washed sand at the surface. If the vegetation on that terrace was removed in the 1860's, then the early phase was complete and junipers were establishing after 40 yrs.

We have little data that show the impact of large floods, such as the 1891 flood and the 1938 flood, which had recorded flows estimated at half the magnitude of the 1862 flood. It may be that the terrace between the junipers was reworked and flushed in either or both of these floods, thereby extending the early and intermediate stages of succession.

The complex nature of alluvial terraces and the changes that occur with succeeding floods of differing magnitudes make it essentially impossible to map in detail the vegetation of the upper Santa Ana River with regard to successional status. There are many areas where the general vegetation is in the mature phase but small recently eroded channels form fingers of early successional habitats as narrow as 1 or 2 m wide.

The sensitive nature of alluvial scrub species composition to changes in clay, silt, and organic matter suggests that airborne dust from mining operations, construction, or other activities settling in alluvial scrub habitats results in a relatively rapid (within 40 yrs) accumulation of fines and organics decreasing the permeability of the original sand deposits (McFadden and Weldon II 1987) and, as a result, may possibly contribute to the changes in species composition, as was also suggested by McBride and Stone (1976) for sand dune habitats. Because this would shorten the time that this increasingly rare community can persist between floods, this topic merits additional investigation.

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